THE VARIABLE DESERT

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SINCE 1903, the Desert Botanical Laboratory of the Carnegie Institution of Washington has served as a base for field excursions for many scientific men—not botanists merely, but geographers, geologists, physiographers, climatologists, zoologists and anthropologists. These men have come into personal contact with the southwestern deserts and have looked upon inert and living features with eyes trained for the most diverse sorts of details. Many of them have set forth in popular as well as in technical terms their impressions of these vast and scientifically fascinating regions of our national territory. To add another to the excellent descriptions of the region available from the pens of Coville, McGee, Hornaday, Huntington, Lloyd, Spaulding and MacDougal would be quite superfluous were it not for the fact that none of these men have, as it seems to me, emphasized in a few paragraphs the one essential feature of our southwestern deserts, which makes them possibly the best naturally equipped experimental laboratories which have been placed within the reach of American students of living things.

The striking characteristic of this whole region is heterogeneity, variability, contrast—whichever one may wish to call it. This is manifest in every fundamental element of the environmental substratum—geographic, physiographic, climatic, edaphic and biologic. Its consequences are discernible in every feature of the biological superstructure—floristic, morphologic, physiographic and genetic.

To the average reader, the word desert calls up the mental picture of a region of bare rocks and dry wind-swept sand, inhospitable to any but the toughest plant and intolerable to any but the hardiest animal. Such a desert presents to the imagination a landscape of the direst monotony—a landscape exactly the opposite of that of our southwestern deserts, which are filled with diversity and interest.

Geologically, the deserts of the general region of Tucson consist of a number of rugged mountain groups, varying greatly in age and composition, with their long detrital slopes and the alluvial valley of the Santa Cruz.

Biologically, the topography of a region is generally a far more important factor than its composition. Within easy reach of the Desert Laboratory are three ranges of mountains with elevations of 9,000 feet or over. Thus within a few miles of the lowest point in the Santa Cruz

valley there is a rise of roughly 6,500 feet. This necessarily means great variety of topography.

The biological covering of so diversified a terrain would be highly differentiated even in a region of the earth's surface in which rainfall is ample in amount and uniform in distribution. Here, irregularity and violence of rainfall is superimposed upon irregularity of surface and plays its part as a powerful environmental factor.

Leaving Tucson by any of the chief highways, one finds himself at once in vast stretches of mesa or of rocky slopes, showing everywhere the most striking marks of water action. To find a xerophytic vegetation in a region where records of water action are so conspicuous is a great surprise to the novice; yet the one is really the logical consequence of the other.

The twelve inches, more or less, of annual rainfall are divided between a season of gentler winter showers and another of torrential summer rains. The former leave very little evidence of their occurrence on the landscape. The latter are often very heavy and their eroding power very great. In one of these, quite unusual, to be sure, five inches of water fell—an amount constituting about half the total precipitation of that year and nearly equal in amount to the total rainfall of the dryest of thirty-one years recorded for Tucson.

The rocky hillsides with only scattered vegetation turn all but a small percentage of the water of these summer cloudbursts into the rocky gulches or canyons, which pass it on to the broad sandy arroyas traversing the long bajadas, transforming both, for a short time, into raging torrents which record their depth by the drift, or even large stones, lodged in the branches of the scrubby trees which mark their courses, in some places many feet above the sandy or gravelly floor, where one fries his bacon and spreads his sleeping bag in the dry season. Past the bajada slopes, the water flows over the broad valleys. Often these are of indeterminate drainage—fine examples of sheet flood erosion. Thus the less precipitous mountain slopes show long ragged gashes cut through the superficial detrital layer to the solid rock beneath, while the fine adobe soil of the apparently flat valleys show here and there areas where the sheet waters have last evaporated, alkali or salt spots, where the drainage is inadequate or sharply carved gutters, where the flatness is only apparent and the gradient really sufficient to give the flowing water considerable cutting power.

With so large a proportion of the total precipitation coming with violence, immediately running off the surface of the steeper slopes and rapidly sinking into the deeper underlying layers in the valleys, physiographic evidence of water action and vegetational evidence of its absence are, in a region of intense heat, inevitable.

This division of the annual precipitation into two periods would

result in marked diversity in the water relations of the plant species, even if the entire amount sank uniformly into the soil. Besides this fundamental source of diversity, there are others.

The amount of water which may fall in each of the two periods, and, indeed, during the whole year, shows great annual variation. The winter and spring showers may be very local. There are not only con-

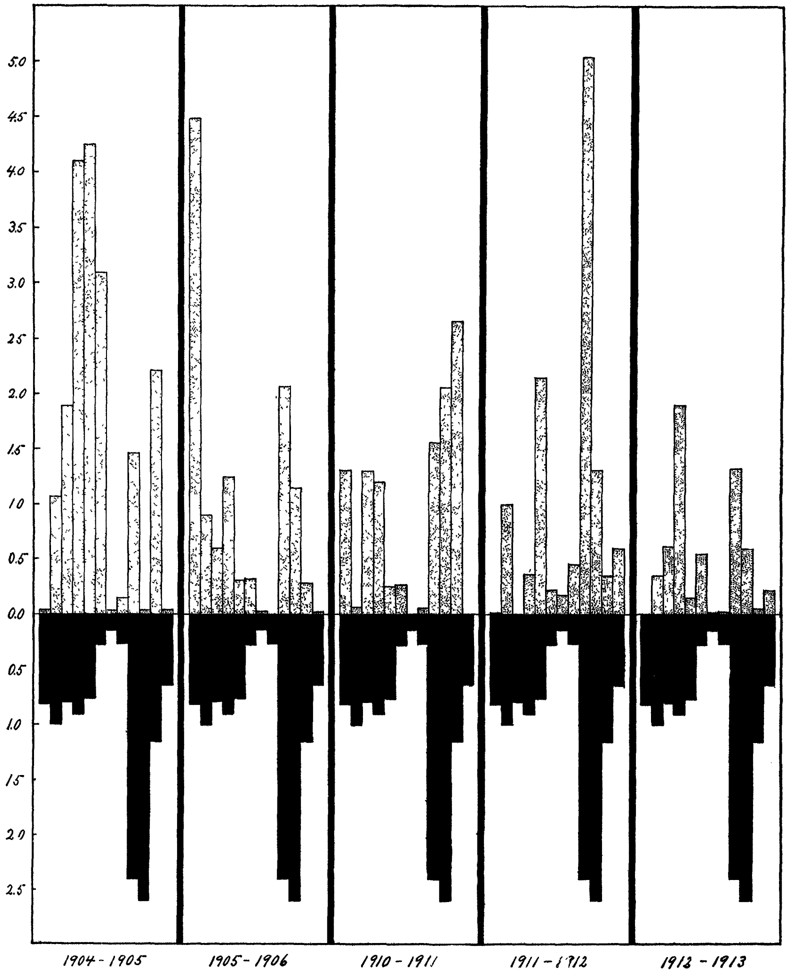

FIG. 1. In this figure are shown the monthly precipitation for five individual periods each of a biological year, beginning with November and ending with October. The rains falling in November and subsequent winter months are chiefly of significance in the development of the winter or spring annuals and in replenishing the reserve of the cacti. The rains falling in October may complete the development of the plants of the second, midsummer, period of growth.

Note that there is not only a division into two distinct rainy seasons which recur annually, but that there is great variation in the amount and time of rainfall from year to year.

The dark area is the average for fifteen years as given by MacDougal. It is repeated under each year to show the extent of variation from the average.

spicuous differences from year to year, but in the same year tracts, only a few hours' ride apart, vary greatly in the state of development of their vegetation.

The soil moisture of a region so variable in rainfall and so diverse in surface topography and in depth and texture (and consequently in water-absorbing power and retaining capacity) as the environs of Tucson, presents a problem of great complexity, even if one considers it from the physical side alone, and not in its more complicated relation to the plant organism.

One must remember that the water which is of service to the plant is not the amount recorded by the rain gauge. Only a portion of the water, falling upon a given spot, may become soil moisture for the plants which grow there. Besides the loss through superficial run off already indicated, there is unquestionably a sub-surface drainage which, when there is sufficient precipitation to bring it about, tends to irrigate some spots at the expense of others. In consequence, there is great variation in soil moisture in habitats otherwise apparently uniform.

By no means all of the water which sinks into the soil can be used. In the development of every plant organism there is a time factor. While physiological processes are carried through with great rapidity in desert plants, there is a minimum beyond which this time element can not be reduced. *Duration* of soil moisture, not merely *absolute amount,* is of great importance.

With regard to the permanence of soil moisture, the various habitats differ widely. Cannon has found that the upper levels of the soil of the bajadas were air dry at the end of three weeks after the rains, while those of Tumamoc Hill and of the Santa Cruz flood plain remained moist for a period exceeding six weeks. On Tumamoc Hill, the superficial soil layer may be so thoroughly baked during the dry fore-summer that the water content falls to about 2 per cent. of its volume; but beneath, the water supply is probably adequate for the growth of the more hardy and deeper-rooted shrubs, throughout the periods when other conditions are favorable. Anomalous as it may seem, the great evaporating power of the air is the cause of the retention of the considerable quantities of moisture in the lower layers of the soil—at a depth available to many perennials and in amounts sufficient for life and even growth during dry seasons. From the surface layers, evaporation is so rapid after a rain that a dry mulch is formed, preventing more or less effectively the loss of water from beneath.

Temperature shows not merely a fluctuation of over 100 degrees Fahrenheit during the year, *all falling above zero,* but great diurnal variation as well. In the growing and even flowering season of the winter annuals, the days are warm—or hot, in the terminology of the more temperate regions,—while the nights have freezing temperature.

A skim of ice may form over one's aluminum drinking cup at breakfast before he breaks camp to collect the earliest flowering winter annuals.

Topographic irregularities greatly complicate temperature relationships. Southern species may have their northernmost limits of distribution on the southwestern slopes of the rocky hills. Here the temperature is far higher than over the crests where cold winds sweep against their northern slopes. It is in such localities that the splendid organ cactus, or pitahaya, flourishes, apparently beyond its reproductive limits, in the Cababi hills.

FIG. 2. Northeasternmost limit of the Organ Cactus, or Pitahaya, in a protected valley of the Cababi Hills about seventy-five miles southwest of Tucson, opening towards the Mexican desert. Here it is growing among the columnar giant cacti and a thick stand of half shrubs which are characteristic of the rocky slopes.

It is in these deserts that the temperature environments, which one might predict, from commonly accepted rules, are apt to be modified by the phenomenon which MacDougal has designated as Cold Air Drainage. During the night the air from higher levels, becoming cooled, flows down the rocky slopes through the canyons, where it may form true aereal rivers, and into the valleys where it lowers the night temperatures of the plant organisms.

The naturalist, trained in a region where there is not a great diurnal heating of the earth's surface and a rapid nocturnal radiation of heat from a rocky dry soil, relatively unprotected by vegetation, is apt to think of this factor as one that might be demonstrated to exist only by long series of exact instrumental observations. On the contrary, the phenomenon is readily appreciable. A beautiful demonstration is to be seen from Tumamoc Hill. In the early morning, the broad valley of the Santa Cruz seems filled with fog. This is really the mesquite smoke of Tucson carried down by the cold air drainage from the higher-

lying plains towards the Gila Valley to the northwest. Above the village, the smoke curls high and irregular; below, it is drawn into the cold air current and borne down the valley in a stream whose upper limits seem marked off along the bajadas of the Santa Catalinas with almost the linearity of the draftsman's T-square.

Shreve has shown that the temperatures in the valley may, in consequence of this factor, be many degrees below those of the hill.

When the temperature becomes sufficiently high—although absolutely it is very low—for the germination of the winter annuals the soil is apt to contain a moderate amount of moisture, at a little distance below the surface, but remains always at a relatively low temperature. Thus, although the soil surface and the sub-aereal parts of the plant (the stems and leaves) may be exposed to rather intense heat during the day, the more deeply penetrating roots are subjected continuously to the retarding influence of low temperature, while the shoots must carry on their physiological activities under the influence of alternating high and low temperatures.

The summer annuals, on the other hand, germinate after the rains have not only soaked but cooled the superficial layers of a substratum which has been both dried and heated to a great depth by the intense insolation of the fore-summer. Thus, their roots develop under conditions of favorable temperature at least, and generally of both temperature and moisture. The summer rains cool the air and change the atmosphere conditions from those of intense heat and enormous evaporating power to those of high relative humidity. Thus there is a brief period of optimum conditions for the luxuriant growth of plants with extensive leaf development. Relative humidity may range from 10 per cent. to saturation. In its relation to the evaporating power of the air and consequently to transpiration, variation in relative humidity is a factor of fundamental biological significance.

Such, briefly, are the salient physical features of the region. It is evident that the plants which inhabit it must derive their water from rainfall, not only meager in quantity, but irregular in local and temporal distribution, and which fails, to a great and highly variable extent, to penetrate into the substratum. This moisture they must draw from a soil irregular in depth and texture and in water-holding capacity and sometimes highly impregnated by mineral salts. Saturation of the soil for brief periods is followed by a condition of complete dryness in most localities. In others, deep-rooted species may obtain water throughout the year. All their physiological processes must be carried out under widely ranging temperatures. Their aereal shoots are exposed to intense insolation in an atmosphere which is generally dry, and often moving at a considerable velocity. Brief periods of high relative humidity may alternate with those of excessive evaporating power of the air.

Thus in every factor there is conspicuous environmental heterogeneity or variability. What are the consequences for living organisms?

First of all, the distribution of the rainfall in two seasons separated by a period of intense heat and dryness, in a region affording sufficient temperature for growth throughout the greater part of the year, results in two distinct vegetative seasons. The first is the period of winter and spring annuals, shrubby or frutescent perennials. The second is that of summer annuals and frutescent and arborescent perennials.

The annuals developing in the winter and spring months and those appearing after the torrential rains during the heat of July and August are not only subjected to widely different conditions of growth, but are specifically distinct and physiologically dissimilar. The life cycle of these winter annuals may be short or long, depending upon the distribution of temperature. They may germinate and begin growth with November rains and mark time in development throughout the colder winter months, and complete vegetation and fruition with the precipitation of February and March and the warmth of March and April. On the other hand, germination and initial growth may be delayed by low temperature and inadequate moisture until well into March, when, if water is scarce and temperature high, the whole life cycle of the plant may be of remarkable brevity. Under these circumstances, many of the plants open their flowers and even nearly or quite mature their fruits with the cotyledons still apparently functional.

If the winter rains be supplemented by heavy spring showers, the winter annuals, which would otherwise be dwarfed, except in the most favored spots, may show long-continued growth and attain a large size.

While the winter and summer annuals pass the periods of greatest extremes of temperature and of dryness in the form of resistant seeds, the woody perennials must remain exposed to the most extreme conditions of the year. In their physiological activities, they show the greatest diversity. Some respond to the winter moisture and spring warmth by foliation and fruition. Others lie dormant throughout the first growing season to burst into leaf and flower after the heavy summer rains. Some are physiologically active in one growing season only, others in both. *Fouquieria* loses its tender leaves whenever the soil becomes too dry, and clothes itself with green again, whenever temperature and soil moisture are favorable. *Mortonia* retains its tough leaves for years.

The second consequence of the division of the rainfall into two seasons, instead of one period of precipitation, usually found in desert regions, is a fairly luxuriant growth of tree-like perennials, as well as of small rapidly maturing annuals. Thus, these southwestern deserts have fittingly been called arboreal deserts; the greenest of all deserts.

It is this covering of trees, often mere shrubs, if size be the criterion

FIG. 3. Spreading arborescent cactus, *Opuntia* sp. growing near Hayes's Well, about forty miles southwest of Tucson. Mesquite trees in the background. The grass in the foreground is unusually abundant. Photograph by Dr. MacDougal.

of classification, but trees, properly so called, if age be taken into account, which takes away the monotony of the stones, gravel and adobe, only to replace it for the average traveler by a monotony of cacti, yuccas and agaves, scattered shrubby bushes or small trees—for the smaller plants are seen only at limited seasons of the year and are commonly not visible from the Pullman window.

FIG. 4. Young giant cacti or Sahuaros growing among spinose ligneous plants. Note the more mature giant cacti and mesquite trees in the background and the smaller shrubs and the procumbent platyopuntas in the foreground where the mesa floor is bare of most other vegetation. Photograph by Dr. MacDougal.

But the subjective monotony of the traveler has no objective reality in the paucity of conspicuous forms. Among the cacti, there are the generally procumbent flat-stemmed opuntias, or prickly pears, the shrub or tree-like round-stemmed opuntias, *Cylindropuntias,* or *chollas,* the barrel cacti, or bisnagas and above all the splendid fluted columns of the giant cactus or *sahuaro.* The latter is represented by but a single species, but there are five or six quite distinct and highly interesting round-stemmed cacti that are indifferently called *chollas* and a score of species of prickly pears and other cacti that can not be distinguished from a distance. When leafless, two acacias will not be distinguished by the novice from the mesquite belonging to quite a different genus. Add to these the palo verde, the ocatillo, the yuccas and agaves, *Dasylirion,* the omnipresent creosote bush and several other shrubs, which are less dominant in the facies of the vegetation: a respectable beginning, then, has been made upon a rather thick flora of the region.

In fact, the flora is not at all meager. The paucity of species is only apparent; it arises from the facts that only the more conspicuous ones are seen at all by the average tourist, that things which are quite distinct are liable to be confused, that those which do occur together in the same plant association are not all in a vegetative condition, and hence not easily distinguished by the novice, at the same time.

Standing as it does in a transition zone between the highlands of New Mexico and of northern and eastern Arizona and the great desert that stretches away southwest to the Colorado delta, with the valley of the Santa Cruz connecting it with the Sonoran Highlands on the south, with the diversity in environmental conditions which accompany a range of elevation of several thousands of feet within a radius of but a relatively few miles, it is inevitable that this region would exhibit a marvelous commingling of taxonomically and floristically diverse plant organisms.

The bare statement that the region contains a flora rich in genera and species and of diverse geographic origin or affinity is entirely inadequate as a description of its real biological diversity. The plants which one sees are of the most highly contrasted structural types.

Some few species have roots extending far down to a permanent water supply, in the few places where this is possible, others have a spreading underground system lying immediately beneath the surface. Growing side by side, one may see large bisnagas or magnificent sahuaros, whose stems contain hundreds or thousands of liters of water and hard dry-stemmed shrubs. During the brief moist seasons, plants with leaves as tender as those of our eastern forests hasten through their development in the shade of tiny-leaved trees, many of which, notwithstanding their small size, were old before the Spanish came down through the valley of

the Santa Cruz. Rooted in the same soil, one may find species whose juice shows high and others whose cell sap shows low concentrations.

Thus diversity or differentiation in the living organisms is not structural merely. After a few weeks in the field, the observer will realize, more fully than he has ever before, that the distinctions between species are not solely of the kind that can be drawn or photographed or ascertained by inspection of that sacred and indispensable mummy, the type specimen. The species of plants are not merely externally dissimilar, but inherently very diverse; they are not merely morphologically differentiated but physiologically very distinct; they are to be distinguished not merely by their external form, but by their methods of reaction to the various factors of their environment.

In the greatest variety of ways these morphological and physiological differences are exhibited. Many of these have been briefly indicated in foregoing paragraphs. To enumerate in greater detail, the diverse modifications of the structural elements of which the flowering plant is typically built up or the variety of response to environmental factors would carry us too far into technical descriptions.

It is this great complexity of environment and this diversity of organisms which render the southwestern desert one of the most fascinating and profitable of all regions to the biologist, whether by specialization taxonomist, morphologist, physiologist or evolutionist.